

## Darwin's bark spider: giant prey in giant orb webs (*Caerostris darwini*, Araneae: Araneidae)?

Matjaž Gregorič<sup>1</sup>, Ingi Agnarsson<sup>2</sup>, Todd A. Blackledge<sup>3</sup> and Matjaž Kuntner<sup>1</sup>: <sup>1</sup>Institute of Biology, Scientific Research Centre, Slovenian Academy of Sciences and Arts, Ljubljana, Slovenia. E-mail: matjaz.gregoric@gmail.com;

<sup>2</sup>Department of Biology, University of Puerto Rico, San Juan, Puerto Rico, USA; <sup>3</sup>Department of Biology and Integrated Bioscience Program, University of Akron, Akron, Ohio 44325-3908, USA

**Abstract.** Although the diversity of spider orb web architectures is impressive, few lineages have evolved orb webs larger than 1 m in diameter. Until recently, such web gigantism was reported only in a few nephilids and araneids. However, new studies on bark spiders (*Caerostris*) of Madagascar report a unique case of web gigantism: Darwin's bark spider (*C. darwini*) casts its webs over substantial water bodies, and these webs are made from silk whose toughness outperforms all other known spider silks. Here we investigate *C. darwini* web architecture and provide data to begin to answer two intriguing questions to explain these extraordinary web characteristics: 1) Are *C. darwini* webs specialized to subdue unusually large, perhaps even vertebrate, prey? 2) Do these large, riverine webs allow the spiders to capitalize on catching numerous small semi-aquatic insects? During fieldwork in Madagascar, we studied *C. darwini* web architecture and ecology, as well as interactions with prey. We characterize *C. darwini* webs as having relatively simple capture areas with very open sticky spirals and few radial lines. We also compare web features in several sympatric *Caerostris* species, among which *C. darwini* represents the most extreme case of web gigantism, with the largest orbs up to 2.76 m<sup>2</sup> and longest bridge lines reaching 25.5 m. While preliminary, current data suggest that *C. darwini* webs are effective snares for semi-aquatic insects such as mayflies and dragonflies, while vertebrate prey were never observed. We suggest that mass emergence of aquatic insects may function analogously to the capture of rare, large prey that recent studies suggest are critical for reproduction in orb weaving spiders.

**Keywords:** Web gigantism, web architecture, web size, bridge line, kleptoparasite, silk, biomaterial, prey capture

Spider orb webs are highly efficient and specialized traps that have diversified greatly through time (Eberhard 1982; Coddington 1986a; Coddington & Levi 1991; Blackledge et al. 2009, 2011; Foelix 2011; Herberstein & Tso 2011). In addition to the classical “wagon-wheel” shaped orb itself, derived web forms include linyphiid sheetwebs and theridiid cobwebs (Griswold et al. 1998; Agnarsson 2004; Eberhard et al. 2008), uloborid and araneid sector webs (Wiehle 1927; Gregorič et al. 2010), nephilid and araneid ladder webs (Robinson & Robinson 1972; Eberhard 1975; Harmer & Framenau 2008; Kuntner et al. 2008a, b, 2010b; Harmer 2009), the deinopid casting web (Coddington 1986b) and others. Even for “standard” orb webs, the details of architecture and overall web size also vary substantially among taxa and include several instances of “web gigantism”. For example, webs within the family Nephilidae encompass extremes ranging from small arboricolous ladders in *Cliataea* Simon 1889 to the dramatically elongated ladder webs of *Heremnia* Thorell 1877 and *Nephilengys* Koch 1872, which often exceed a meter in height (Kuntner 2007; Kuntner et al. 2008a, b, 2010; Kuntner & Agnarsson 2009), and the giant aerial orbs of *Nephila* that reach 1.5 m diameter (Kuntner et al. 2008a). The largest known orb webs are built by the recently described Darwin's bark spider *Caerostris darwini* (Kuntner and Agnarsson 2010) from Madagascar. These spiders produce webs close to 2 m in diameter that are suspended upon the longest bridge lines ever recorded, allowing the webs to span rivers and small lakes (Agnarsson et al. 2010; Kuntner & Agnarsson 2010).

Bark spiders (genus *Caerostris* Thorell 1868) are a diverse group, widespread in the old world tropics, that are poorly studied taxonomically, ecologically and behaviorally (Kuntner & Agnarsson 2010). Grasshoff (1984) revised this genus, but

its phylogenetic placement remains controversial (Scharff & Coddington 1997; Kuntner et al. 2008a; Sensenig et al. 2010). Only 12 *Caerostris* species are currently considered valid (Platnick 2010; Kuntner & Agnarsson 2010).

The most recent studies on *Caerostris* of Madagascar hint at further, as yet undescribed diversity (Kuntner & Agnarsson 2010). Up to seven sympatric species inhabit a single reserve, the Andasibe-Mantadia National Park. Some of these species are nocturnal and others diurnal, but almost all of them construct sizeable webs at forest edges or clearings (Agnarsson et al. 2010; Kuntner & Agnarsson 2010). However, one species, the recently described Darwin's bark spider, *C. darwini* (Fig. 1) exhibits exceptional web biology and behavior in utilizing a unique habitat by building webs above streams, rivers and lakes (Fig. 2A–C; Kuntner & Agnarsson 2010). These webs can reach extreme sizes – suspended between vegetation on the riverbanks by bridge lines that often span more than 10 m, with the orbs frequently exceeding 1 m in diameter (Kuntner & Agnarsson 2010). A second, apparently undescribed, *Caerostris* species in Andasibe-Mantadia NP also builds its webs over water, but only spanning relatively small streams inside closed canopy forest. Although other spiders build webs on edges of water bodies, or even attach webs to water (Eberhard 1990), individual spiders in no other species routinely utilize the air column above large streams, rivers and lakes as a habitat (Kuntner & Agnarsson 2010). How the spiders cross these large water bodies is only now being researched (Gregorič et al. in prep.), but *C. darwini* webs are constructed of silk that outperforms all other spider silks in combining high strength and elasticity into the toughest known biological material, outperforming even most synthetic fibers (Agnarsson et al. 2010).

Thus, it is certainly desirable to expand our understanding of *Caerostris* biology, in particular of key species such as

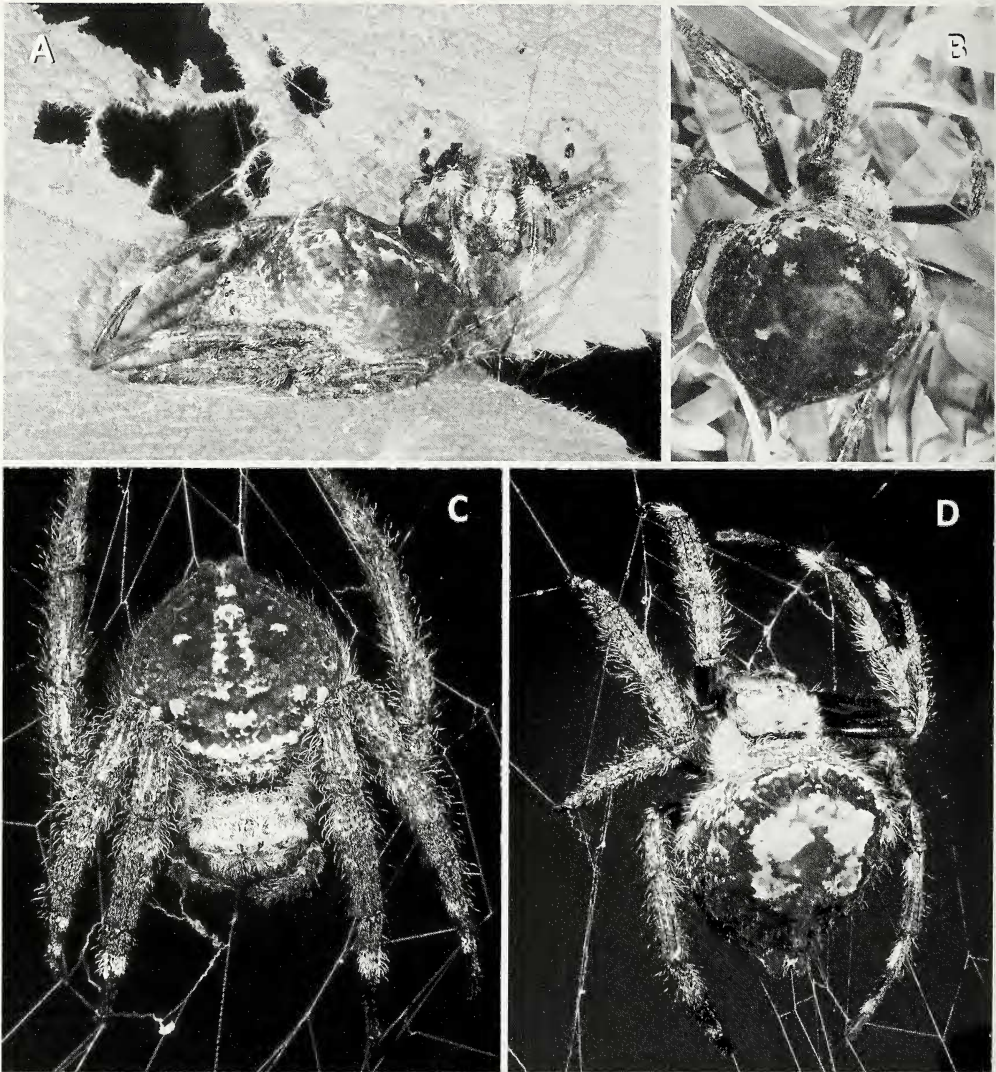


Figure 1.—*Caerostris darwini* in Andasibe-Mantadia NP: A, male with female in vegetation; B–D, females with typical color (C) and two less common color forms (B, D).

*C. darwini*. In this paper, we broaden knowledge of *C. darwini* natural history by characterizing their webs, including a comparison with three congeners. We also begin to test whether or not their giant riverine webs are specialized for capturing exceptional prey. The combination of web gigantism and the high material toughness of *C. darwini* silk, as well as

the webs' location across rivers that could act as flyways, suggests that these webs could be specialized in part for capture of small flying vertebrates – birds or bats (Agnarsson et al. 2010; Kuntner & Agnarsson 2010). Both birds and bats are occasionally captured in the webs of several species of orb spiders (Levi 1970; Graham 1997; Peloso & de Sousa 2007;



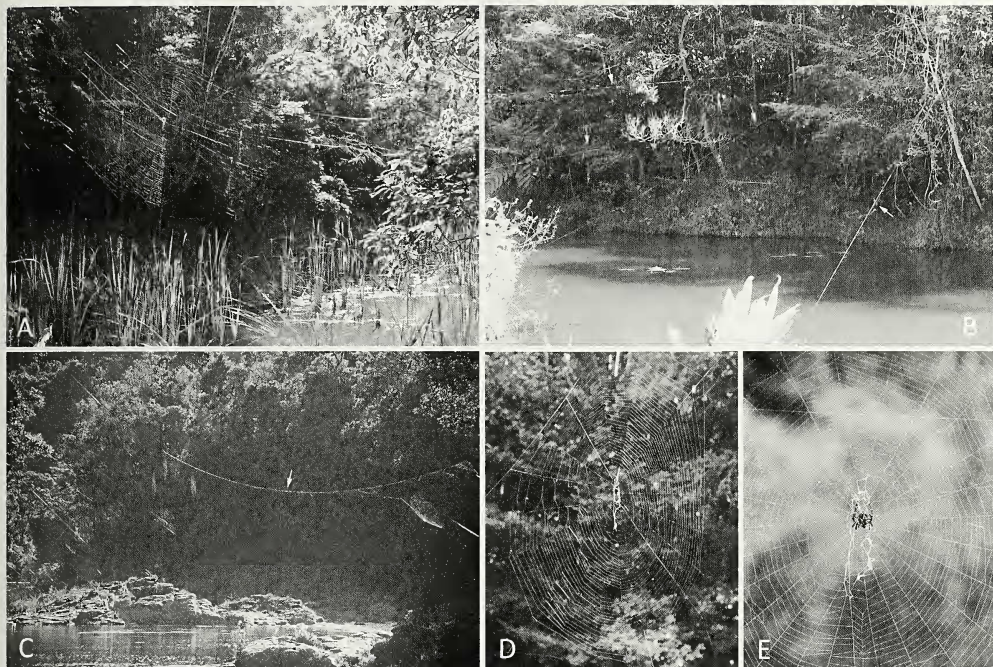


Figure 2.—*Caerostris darwini* habitat and prey: webs suspended above water in Ranomafana NP (C) and Andasibe-Mantadia NP with whole orbs (A) and only bridge threads (B) visible; *C. darwini* female with a robust (D) and a rudimentary (E) stabilimentum in web.

Sakai 2007; Timm & Losilla 2007). Sensenig et al. (2010) used web architecture and silk biomechanics to estimate that *C. darwini* webs could resist up to  $62 \mu\text{J}/\text{cm}^2$  of prey energy without breaking during impact, which approaches the flight energy of some birds and bats, the smallest of which are less than 2 g body mass and fly at speeds less than 5 m/s. Alternatively, or additionally, *C. darwini* webs could present large surface areas for the simultaneous capture of numerous aquatic insects, especially during mass emergences.

#### METHODS

**Field site.**—We studied *C. darwini* and three other syntopic *Caerostris* species (labeled as “sp. 1”, “sp. 2” and “sp. 3”) in Andasibe-Mantadia National Park (between  $18.94760^\circ\text{S}$ ,  $48.41972^\circ\text{E}$  and  $18.79841^\circ\text{S}$ ,  $48.42631^\circ\text{E}$  at  $\sim 960$  m elev.), Toamasina Province, eastern Madagascar, on 24 February 2010–4 April 2010. Voucher specimens are deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, DC.

**Behavioral recording.**—We video recorded and photographed prey capture behavior and web architecture using camcorders (Sony DCR-SR87 HDD) and SLR cameras (Canon EOS 5D Mark II and EOS 7D).

**Web characteristics.**—To measure how long *C. darwini* webs persisted, we monitored 20 webs of mature females for three

days and documented web building time. We also quantified web parameters for an additional 26 mature females' webs illustrated in Fig. 3a–c as well as length of bridge line (Fig. 2B, C), number of radii, number of sticky spirals (SS) along the vertical axis, number of kleptoparasitic spiders associated with the web, stabilimentum (defined as absent (0), rudimentary (1) or robust (2) (Fig. 2D, E)), habitat (defined as above water (0) or not above water (1)), canopy (defined as open (0) or closed (1) if estimated that more than 50% of the canopy was covered by tree crowns). Most of the above parameters have been used previously in the literature (e.g. Risch 1977; Opell 1999; Herberstein & Tso 2000; Blackledge & Gillespie 2002; Kuntner et al. 2010; Kuntner & Agnarsson 2009; Gregorić et al. 2010; Nakata & Zschokke 2010).

To quantify web shapes, we then calculated indices following Peters (1937), Blackledge & Gillespie (2002), and Kuntner et al. (2008b): Web capture area (CA) was defined by the formula:

$$CA = (a/2) * (b/2) * \pi$$

where *a* and *b* were the horizontal and vertical diameters, respectively, of the capture area. Mesh width was defined as the number of rows of SS per centimeter of web height.

We calculated a ladder index (LI) or vertical eccentricity of capture area as:

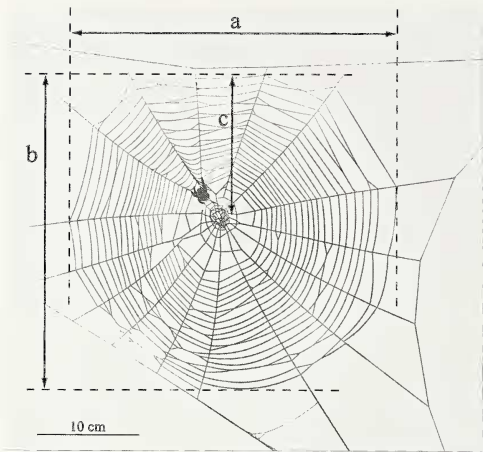


Figure 3.—Web of female *Caerostris darwini* illustrating investigated parameters: web width (a), web height (b) and top sticky spiral to hub distance (c).

$$LI = b/a$$

We also determined vertical web asymmetry through hub displacement index (HD) as:

$$HD = (b - c)/b$$

where  $c$  was the distance from the center of the hub to the bottom of the capture area.

For an additional comparison of web size, we measured web width, height, top sticky spiral to hub distance, and bridge length in *Caerostris* “sp. 1” ( $n = 16$ ), “sp. 2” ( $n = 22$ ) and “sp. 3” ( $n = 5$ ). We then compared our data with published data for web sizes of other orb weaving spiders, limiting ourselves to webs of at least  $0.1 \text{ m}^2$  (Table 1).

**Prey capture.**—To document prey capture, we recorded every wrapped or fed upon prey item in *C. darwini* webs. Additionally, we video recorded four spiders during the daytime for four days each, for a total of 113 h. Because the video resolution precluded exact determination of prey taxa, we grouped prey items into three size categories: small ( $< 1 \text{ cm}$ ), medium (1–2.5 cm) and large ( $> 3 \text{ cm}$ ).

Based upon an analysis of web architecture and silk biomechanics, Sensenig et al. (2010) estimated that *C. darwini* webs could stop higher energy flying prey than a phylogenetically diverse sampling of 16 other genera of orb spiders, including other large orb-weavers such as *Nephila* and *Argiope*. However, their estimate is a theoretical measure of maximum performance, which may not be attained by actual webs, and they also did not measure how effectively the webs could retain prey. To better determine the maximum prey size that *C. darwini* webs can stop and retain, and to document the spiders’ attack behavior, we introduced 34 medium and large prey items, each into a different web. Prey included five grasshoppers (2 cm), one large grasshopper (5 cm), one mantis

(10 cm), two small frogs (2 cm), two moths (10 cm), two beetles (7 cm), 13 small dragonflies of different species (4–7 cm), and eight large (10 cm) dragonflies of one species. Prey were tossed into the capture areas of webs from a distance of  $\sim 0.5 \text{ m}$ , more or less with the same speed and more or less perpendicular to the web plane. Although the initial impact of prey with the web using this technique did not perfectly mimic natural interceptions and we could not control for how many threads each prey contacted, our method should still provide a reasonable index of the ability of *C. darwini* webs to stop and retain several different types of potential prey.

**Statistical analysis.**—We checked all data for normality using Kolmogorov-Smirnov tests. Because the distribution of data was not normal for bridge length and web area, we report medians ( $\mu_{1/2}$ )  $\pm$  interquartile ranges for these parameters, while we report mean values ( $A$ )  $\pm$  standard deviations for other data. We tested interspecific differences in web measures using the Kruskal-Wallis test and Mann-Whitney U-tests. We set the significance level to 0.008 or lower (Bonferroni correction). We performed all analyses in PASW 18 for Windows (Field 2005).

## RESULTS

**Web characteristics.**—*Caerostris darwini* orbs ranged in size from  $0.21 \text{ m}^2$  to  $2.76 \text{ m}^2$  ( $\mu_{1/2} = 0.61 \pm 0.52 \text{ m}^2$ ). Capture area did not significantly differ from those of *Caerostris* sp. 1 and *Caerostris* sp. 2 ( $\mu_{1/2} = 0.48 \pm 0.21 \text{ m}^2$  and  $\mu_{1/2} = 0.5 \pm 0.39 \text{ m}^2$ , respectively), whereas *Caerostris* sp. 3 had a significantly smaller capture area ( $\mu_{1/2} = 0.16 \pm 0.1 \text{ m}^2$ , Fig. 4). Bridge lines of *C. darwini* orbs were  $0.95\text{--}25.5 \text{ m}$  ( $\mu_{1/2} = 3.5 \pm 2.6 \text{ m}$ ), significantly longer than those of other *Caerostris* species ( $\mu_{1/2} = 1.7 \pm 1.1 \text{ m}$  in sp. 1;  $1.8 \pm 1.2 \text{ m}$  in sp. 2 and  $1.4 \pm 0.67 \text{ m}$  in sp. 3; Fig. 4). The webs of *C. darwini* contained 15–30 radii ( $A = 23.5 \pm 4$ ), no spiral radii, 40–155 vertical SS ( $A = 97 \pm 25$ ) and mesh widths of  $0.51\text{--}1.7 \text{ SS/cm}$  ( $A = 1.04 \pm 0.33$ ). All webs lacked secondary radii (Kuntner et al. 2008a), and only two (8%) webs had stabilimenta (both “rudimentary”). The webs were almost symmetric with the ladder index of  $0.78\text{--}1.49$  ( $A = 1.19 \pm 0.18$ ) and hub displacement of  $0.47\text{--}0.69$  ( $A = 0.59 \pm 0.05$ ). Most (63%) webs did not contain kleptoparasitic spiders. Four (21%) webs contained one or two kleptoparasites (all Argyrodinae), whereas only three (16%) webs contained more.

All webs were suspended above or at the edges of water bodies and always under open canopy (Fig. 2A–C). The webs never had retreats, and the spiders sat at the hub during all weather conditions (not removing SS during rain), day and night. Our monitoring of 20 webs over 3 days revealed that the webs were not long lasting. In two of these 20 webs, the host spider was absent for the whole time, and two more spiders disappeared during observation. The other 15 spiders renewed their webs two to four times in 3 days. Web renewal usually (74%) took place between 1600 and 1800 h. However, throughout our fieldwork we observed numerous webs being constructed at the same location, suspended on bridge lines that were clearly retained for several days. We thus estimated that bridge lines can be maintained for at least 5 wk. We never observed web destruction by flying vertebrates or large insects, but regularly observed dragonflies avoiding the webs and even perching on bridge lines.



Table 1.—Comparison of web size (if > 0.1 m<sup>2</sup>) among orb web spiders, measured for adult and penultimate female webs.

Species	Web area (m <sup>2</sup> )	Max. web area (m <sup>2</sup> )	Author
<i>Metellina merianae</i> (Scopoli 1763)		0.28	Wiehle 1927
<i>Argiope katherina</i> Levi 1983 ( <i>n</i> = 24)	0.13	0.22	Rao pers. comm.
<i>Herennia etruscilla</i> Kuntner 2005 ( <i>n</i> = 2)	0.13	0.14	Kuntner et al. 2010b
<i>Talthybia depressa</i> Thorell 1898 ( <i>n</i> = 1)	0.21	0.21	own data
<i>Eriovixia laglazei</i> (Simon 1877) ( <i>n</i> = 1)	0.32	0.32	own data
<i>Nephilengys dodo</i> Kuntner & Agnarsson 2011 ( <i>n</i> = 2)	0.44	0.56	own data
<i>Caerostris sumatrana</i> Strand 1915 ( <i>n</i> = 1)	0.62	0.62	own data
<i>Herennia multipuncta</i> (Doleschall 1859) ( <i>n</i> = 6)	0.11 ± 0.2	0.29	Kuntner et al. 2010b
<i>Nephila inaurata</i> (Walckenaer 1841) ( <i>n</i> = 23)	0.12 ± 0.28	1.15	own data
<i>Argiope radon</i> Levi 1983 ( <i>n</i> = 103)	0.122 ± 0.055	0.49	Rao et al. 2009, pers. comm.
<i>Argiope argentata</i> (Fabricius 1775) ( <i>n</i> = 762)	0.13 ± 0.045		Nentwig 1985
<i>Araneus angulatus</i> Clerck 1757	0.13–0.31	0.31	Wiehle 1929
<i>Araneus circe</i> (Audouin 1826)	0.13–0.28	0.28	Wiehle 1928, 1931
<i>Nephila clavipes</i> (Linnaeus 1767) ( <i>n</i> = 32)	0.15 ± 0.07	0.35	own data
<i>Caerostris</i> sp. 3 ( <i>n</i> = 5)	0.16 ± 0.1	0.35	this study
<i>Nephilengys borbonica</i> (Vinson 1863) ( <i>n</i> = 4)	0.19 ± 0.09	0.23	own data
<i>Nephila ardentipes</i> Butler 1878 ( <i>n</i> = 24)	0.19 ± 0.18	0.65	own data
<i>Nephilengys malabarensis</i> (Walckenaer 1841) ( <i>n</i> = 7)	0.23 ± 0.16	0.41	Kuntner et al. 2010b
<i>Eriophora</i> sp. ( <i>n</i> = 20)	0.24 ± 0.18	0.69	own data
<i>Nephila pilipes</i> (Fabricius 1793) ( <i>n</i> = 30)	0.28 ± 0.15	0.63	Kuntner et al. 2010a, own data
<i>Caerostris darwini</i> Kuntner & Agnarsson 2010 ( <i>n</i> = 16)	0.28 ± 0.47	1.07	Kuntner & Agnarsson 2010
<i>Argiope keyserlingi</i> Karsch 1878 ( <i>n</i> = 273)	0.3 ± 0.14		Blamires et al. 2007
<i>Nephilengys livida</i> (Vinson 1863) ( <i>n</i> = 29)	0.33 ± 0.23	0.77	own data
<i>Eriophora fuliginea</i> (C.L. Koch 1838) ( <i>n</i> = 349)	0.36 ± 0.11		Nentwig 1985
<i>Nephila clavipes</i> (Linnaeus 1767) ( <i>n</i> = 1072)	0.36 ± 0.11		Nentwig 1985
<i>Caerostris</i> sp. 1 ( <i>n</i> = 16)	0.48 ± 0.21	0.86	this study
<i>Caerostris</i> sp. 2 ( <i>n</i> = 22)	0.5 ± 0.39	1.1	this study
<i>Caerostris darwini</i> Kuntner & Agnarsson 2010 ( <i>n</i> = 26)	0.61 ± 0.52	2.76	this study

**Prey capture.**—We haphazardly encountered 25 prey items during web surveys: two (8%) honey bees, three small beetles (12%), one wasp (4%), one grasshopper (4%), two damselflies (8%), one fly (4%), one (4%) queen ant, one (4%) butterfly, one (4%) large unidentified prey item, and four (16%) dragonflies. The 113 hours of video material revealed the capture of 50 (79.4%) small, 12 (19%) medium, and one (1.6%) large prey item (a papilionid butterfly). Altogether, large prey items constituted 6.8% of all caught prey; 20% in haphazardly encountered prey and 1.6% in video material, but this disparity is expected because active feeding on small, quickly consumed insects is less likely to be haphazardly observed. Video material also revealed one case of kleptoparasitic flies in *C. darwini* (*Caerostris* supplementary video 3 (<http://www.nephilidae.com/videos/videos.htm>)).

During our prey presentations (*Caerostris* supplementary video 1, 2 (<http://www.nephilidae.com/videos/videos.htm>)), frogs and large insects (i.e., large beetles and moths) were not retained in webs. The webs retained all five 2-cm, but not the 5 cm grasshopper. Out of the 21 dragonflies introduced, the webs retained all 13 “regular sized” specimens, but only four of the eight “large” ones.

All spiders performed bite-wrap attack behavior (*Caerostris* supplementary video 1 (<http://www.nephilidae.com/videos/videos.htm>); Eberhard 1982). The spiders carried all prey, except the largest dragonflies, back to the hub in their chelicerae (*Caerostris* supplementary video 1 (<http://www.nephilidae.com/videos/videos.htm>)), while the large dragonflies were lifted to the hub on a silk thread while still attached

to other parts of web (*Caerostris* supplementary video 2 (<http://www.nephilidae.com/videos/videos.htm>)).

## DISCUSSION

The present study shows that *Caerostris darwini* build the longest bridge lines and largest orb webs known, with exceptional webs bridging water bodies more than 25 m across and capture areas reaching 2.76 m<sup>2</sup> (Tables 1, 2; Fig. 4). *C. darwini* webs contain relatively sparsely spaced capture spirals and are almost symmetrical (Sensign et al. 2010). Webs are always suspended above or next to water and their capture areas are renewed daily. In contrast, bridge lines are maintained and reinforced regularly, for up to five weeks. We found no evidence that these giant webs are an adaptation for capturing flying vertebrates, such as birds or bats. First, no such large prey items were caught in the web, although the sample size in this study is small enough that such rare events could have been missed (Blackledge 2011). Second, numerous visually acute flying insects, such as dragonflies, were seen avoiding the webs throughout the field study. While dragonflies are exceptionally maneuverable fliers (Alexander 1984, 1986; Azuma et al. 1988; Thomas et al. 2004), this observation suggests that flying vertebrates might also perceive and avoid the webs. On the other hand, orb spiders can still capture substantial numbers of insects in taxa that see and avoid spider webs (Craig 1994; Rao et al. 2008). Third, the relatively sparse packing of silk in the webs, which have significantly larger mesh widths than similarly sized orb weavers (Sensign et al. 2010), necessarily limit their stopping and retention

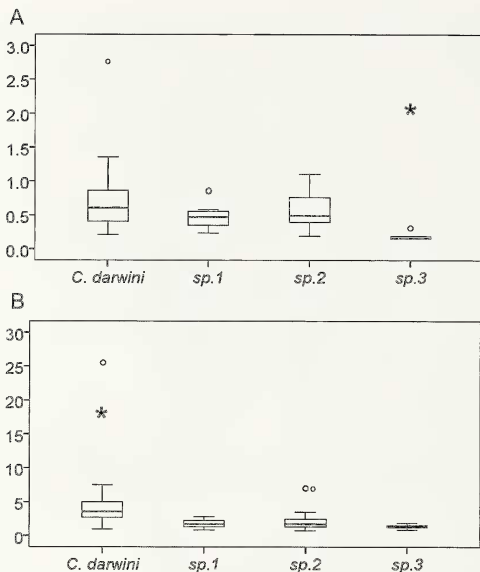


Figure 4.—Web size in *Caerostris darwini* and three congeneric species. A. Web capture area (m<sup>2</sup>). B. Bridge thread length (m). Asterisk marks the species that significantly differ from the others.

power. Instead, along with our previous study, we found that these webs subdue small to large flying insects, such as mayflies (Kuntner & Agnarsson 2010) and dragonflies (this study).

**Web characteristics.**—Although the maximal values of web size are statistical outliers (Fig. 4) in our study, we believe it likely that webs are often even larger in nature. Many *C. darwini* webs are suspended far from the shores of rivers and lakes or high in the air column such that we simply could not measure them. These open, aerial microhabitats are less spatially limited, compared to the more easily accessible space directly above the water surface that we studied. Thus, *C. darwini* may be capable of building larger webs than we measured.

With the exception of their extreme size and unusual microhabitat, *C. darwini* webs resemble typical araneid orbs in many respects (Zschokke 2002; Kuntner et al. 2008a; Kuntner & Agnarsson 2010). They are more or less vertical, almost symmetric, have closed hubs, non-sticky spirals are removed from finished webs, have gradual hub-loop to sticky spiral transitions, have few radii and SS compared to other orb weavers (Sensenig et al. 2010), have no split radii, lack retreats, and rarely contain stabilimenta (Eberhard 1982). Kuntner & Agnarsson (2010) reported the hub as open or closed; however, this is incorrect. We only observed the typically araneid closed hub and the complete lack of the hub bite-out behavior (Gregorić et al. in prep.). Kuntner & Agnarsson (2010) speculated that the webs last longer than typical araneid orbs, but did not have long-term observations of

individual webs over several days. In fact, only the bridge lines are long lasting, while the capture areas are renewed daily as in most other orb weavers (Foelix 1996; Carico 1986). The web building behaviors of *C. darwini* depart from typical araneids (Eberhard 1982; Kuntner 2008a). *C. darwini* exhibit minimal web site exploration and build webs that lack secondary frame threads. The relatively simple capture areas contain very open sticky spirals, supported by few radii that are both single and doubled in the same web. Detailed comparison of web spinning behaviors will be fully summarized elsewhere (Gregorić et al. in prep.).

**Attack behavior.**—*Caerostris darwini* attacks all prey by first biting and then wrapping them. Typical araneid, tetragnathid and uloborid attack behavior is wrap-biting (Eberhard 1982), which probably evolved six to seven times within orbicularian spiders (Kuntner et al. 2008a). In contrast, bite-wrapping is probably plesiomorphic for a larger clade of orb spiders (Kuntner et al. 2008a), and is utilized by nephilids, some araneids such as *Deliochus*, *Phonognatha*, *Caerostris* (Kuntner et al. 2008a) and *Zygiella* s.l. (Gregorić et al. 2010). *Caerostris darwini* uses bite-wrapping regardless of prey size, whereas many wrap-biting spiders occasionally bite-wrap in response to different taxa of prey (Robinson & Robinson 1974; Foelix 1996). *Caerostris darwini* also uses a relatively unusual behavior for transporting subdued prey back to the hub. Instead of freeing large prey from the web and hanging them on a short thread (Foelix 1996), *C. darwini* carries even large prey back to hub in their chelicerae (*Caerostris* supplementary video 1 (<http://www.nephilidae.com/videos/videos.htm>)). Only the largest dragonflies were not carried using this behavior, but instead were lifted toward the hub using a longer silk thread, while the prey was still attached to other parts of web. On the other hand, this observation and the fact that many orb spider species directly carry small prey, suggest that it is the large prey size threshold at which *C. darwini* switches from the carrying behavior that is unusual, rather than the behavior itself.

**Prey capture.**—Our prey tossing experiments found that dragonflies were the largest prey retained by *C. darwini* webs, with larger insects and frogs always breaking through the webs. By far the most commonly observed prey entangled in webs were small insects, with larger (> 3 cm) prey found only at relatively low frequencies (~ 7%). However, the disparity between large prey encountered haphazardly (20%) and by video material (1.6%) is expected because active feeding on small, quickly consumed insects is less likely to be haphazardly observed. Although we never observed exceptionally large prey in *C. darwini* webs, such rare large prey may be fundamentally important for female fecundity in most orb spiders, even though the rarity of their capture makes them difficult to observe in field studies (Venner & Casas 2005; see Blackledge 2011, this volume for review). Therefore, more sampling effort is clearly needed to thoroughly exclude the hypothesis that the unusual size and placement of *C. darwini* webs facilitate the capture of exceptionally large prey.

The rare, large prey hypothesis is particularly tempting, given the exceptional toughness of the silk in *C. darwini* webs (Agnarsson et al. 2010). However, orb spiders face functional tradeoffs between making relatively sparse webs with large capture areas to maximize interception of prey, versus building



Table 2.—Web data for *Caerostris darwini* females in Madagascar. SS = sticky spirals.

	Web area (m <sup>2</sup> )	Bridge length (cm)	Radii no.	SS no.	Kleptoparasite no.	Mesh width (SS/cm)	Ladder index	Hub displacement
	0.21	130	18	40	0	0.70	1.21	0.65
	0.23	265	21	77	0	1.24	1.32	0.55
	0.25	275	20	88	0	1.47	1.15	0.63
	0.26	210	24	104	0	1.70	1.11	0.57
	0.28	330	29	89	0	1.35	1.22	0.53
	0.31	95		0			1.19	0.68
	0.41	320	23	121	0	1.57	1.13	0.60
	0.41	180		53	4	0.71	1.07	0.69
	0.41	400		0			1.07	0.57
	0.46	380	28	110	0	1.33	1.17	0.58
	0.49	164	30	82	7	1.17	0.78	0.64
	0.53	215		0			1.13	0.57
	0.61	350		83	0	0.91	1.06	0.47
	0.62	275	20	110	0	1.12	1.21	0.59
	0.64	300	29	126	6	1.22	1.30	0.58
	0.70	500	25	112	1	1.15	1.05	0.61
	0.76	450	24	103	2	1.03	1.03	0.59
	0.82	670		108	0	0.90	1.38	0.50
	0.86	350	27	91	0	0.73	1.41	0.60
	0.90	430	25	94	0	0.76	1.35	0.60
	1.15	540	23	92	1	0.70	1.19	0.66
	1.19	750		117	1	0.78	1.49	0.60
	1.21	640		83		0.51	1.71	0.58
	1.36	400		0			1.02	0.50
	2.76	550	25	155		0.79	1.08	0.58
		2550						
Sp.1 mean	0.61 ± 0.52	350 ± 260	23.5 ± 4	97 ± 25		1.04 ± 0.33	1.19 ± 0.18	0.59 ± 0.05
Sp.2 mean	0.48 ± 0.21	170 ± 109						
Sp.3 mean	0.5 ± 0.39	177 ± 122						
Sp.3 mean	0.16 ± 0.1	142 ± 66.5						

smaller and denser webs capable of stopping and retaining bigger prey (Chacon & Eberhard 1980; Eberhard 1986; Blackledge & Zevenbergen 2006; Blackledge & Eilason 2007; Sensenig et al. 2010). *Caerostris darwini* web architecture is unusually open, with fewer radii and larger mesh width than other large orb webs (Sensenig et al. 2010). Thus, the webs may instead function to maximize capture surface for large numbers of small aquatic insects, such as the mass capture of mayflies observed in *C. darwini* webs by Kuntner & Agnarsson (2010). Such mass captures could even function analogously to rare, large prey in the rarity of their occurrence and their importance for foraging success. However, no mass capture of insects was observed in this study and might be as difficult to observe during field studies as the capture of individual large prey (Blackledge 2011). Alternatively, the large, sparse capture areas of *C. darwini* webs, combined with their unusually tough silk, may represent a compromise toward subduing large numbers of small aquatic insects while still maintaining the ability to capture rare larger prey. Such a “multifunctional” web would contrast with the behavior of at least one other orb weaver, *Paravixia*, that instead dramatically enlarges capture areas of webs only during mass emergences of large, easily captured reproductive termite prey (Sandoval 1994). The evolution of the extreme silk toughness in *C. darwini* may facilitate this potentially dual function of the large sparse web, making it critical to better determine patterns of evolution for

both silk properties and web architecture within the genus *Caerostris*.

**Conclusions.**—*Caerostris darwini* exhibits several aspects of unusual web biology that allow the spiders to spin giant orbs suspended in the air column above bodies of water, thereby exploiting a unique ecological niche. Prey capture data suggest that *C. darwini* does not prey on flying vertebrates, but instead mostly consumes medium to large flying insects. We speculate that the mass emergence of aquatic insects may function analogously for spider fitness to the capture of single rare, large prey in other orb spiders. However, with the currently available data we cannot rule out alternative hypotheses for the origin of the exceptional properties of *C. darwini* silk, such as adaptation to carry the spiders’ weight on long, sagging bridge lines (Rodriguez-Girones et al. 2010) or resisting abiotic factors such as wind and rain (Eberhard 1990).

#### ACKNOWLEDGMENTS

This is Contribution 1 resulting from the 2010 Madagascar expedition, funded by the National Geographic Society (grant 8655-09 to I. Agnarsson, M. Kuntner, and T. Blackledge). Additional funding came from the Slovenian Research Agency (grants P1-0236, J1-2063) and NSF (IOS-0745379). We thank the MICET crew in Antananarivo, and Sahondra Lalao Rahanitriniaina and Honore Rabarison for their help in the field. We also thank Dinesh Rao, William Eberhard, Sean

Blamires and Wolfgang Nentwig for their help in getting web size data for other spider species.

## LITERATURE CITED

- Agnarsson, I. 2004. Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneioidea, Theridiidae). *Zoological Journal of the Linnean Society* 141:447–672.
- Agnarsson, I., M. Kuntner & T.A. Blackledge. 2010. Bioprospecting finds the toughest biological material: extraordinary silk from a giant riverine orb spider. *PLoS ONE* 5(9):e11234.
- Alexander, D.E. 1984. Unusual phase relationships between the forewings and hindwings in flying dragonflies. *Journal of Experimental Biology* 109:379–383.
- Alexander, D.E. 1986. Wind tunnel studies of turns by flying dragonflies. *Journal of Experimental Biology* 122:81–98.
- Azuma, A. & T. Watanabe. 1988. Flight performance of a dragonfly. *Journal of Experimental Biology* 137:221–252.
- Blackledge, T.A. 2011. Prey capture in orb weaving spiders: Are we using the best metric? *Journal of Arachnology* 39:205–210.
- Blackledge, T.A., M. Kuntner & I. Agnarsson. 2011. The form and function of spider orb webs: evolution from silk to ecosystems. *Advances in Insect Physiology*. In press.
- Blackledge, T.A., J. Coddington, N. Scharff, T. Szuts, J. Wenzel, C. Hayashi & I. Agnarsson. 2009. Reconstructing web evolution and spider diversification in the molecular era. *Proceedings of the National Academy of Sciences USA* 106:5229–5234.
- Blackledge, T.A. & C.M. Eliason. 2007. Functionally independent components of prey capture are architecturally constrained in spider orb webs. *Biology Letters* 3:456–458.
- Blackledge, T.A. & R.G. Gillespie. 2002. Estimation of capture areas of spider orb webs in relation to asymmetry. *Journal of Arachnology* 30:70–77.
- Blackledge, T.A. & J.M. Zevenbergen. 2006. Mesh width influences prey retention in spider orb webs. *Ethology* 112:1194–1201.
- Blamires, S.J., M.B. Thompson & D.F. Hochuli. 2007. Habitat selection and web plasticity by the orb spider *Argiope keyserlingi* (Argiopidae): do they compromise foraging success for predator avoidance? *Austral Ecology* 32:551–563.
- Carico, J.E. 1986. Web removal patterns in orb-weaving spiders. Pp. 306–318. *In* *Spiders: Webs, Behavior, and Evolution*. (W.A. Shear, ed.). Stanford University Press, Stanford, California.
- Chacón, P. & W.G. Eberhard. 1980. Factors affecting numbers and kinds of prey caught in artificial spider webs, with considerations of how orb webs trap prey. *Bulletin of the British Arachnological Society* 5:29–38.
- Coddington, J.A. 1986a. The monophyletic origin of the orb web. Pp. 319–363. *In* *Spiders: Webs, Behavior, and Evolution*. (W.A. Shear, ed.). Stanford University Press, Stanford, California.
- Coddington, J.A. 1986b. Orb webs in 'non-orb weaving' ocrefaced spiders (Araneae: Deinopidae): a question of genealogy. *Cladistics* 2:53–67.
- Coddington, J.A. & H.W. Levi. 1991. Systematics and evolution of spiders (Araneae). *Annual Review of Ecology and Systematics* 22:565–592.
- Craig, C.L. 1994. Predator foraging behavior in response to perception and learning by its prey: interactions between orb-spinning spiders and stingless bees. *Behavioral Ecology and Sociobiology* 35:45–52.
- Eberhard, W.G. 1975. Inverted ladder orb web of *Scoloderus* sp. and intermediate orb of *Eustala* sp. Araneae – Araneidae. *Journal of Natural History* 9:93–106.
- Eberhard, W.G. 1982. Behavioral characters for the higher classification of orb-weaving spiders. *Evolution* 36:1067–1095.
- Eberhard, W.G. 1986. Effects of orb-web geometry on prey interception and retention. Pp. 70–100. *In* *Spiders: Webs, Behavior, and Evolution*. (W.A. Shear, ed.). Stanford University Press, Stanford, California.
- Eberhard, W.G. 1989. Effects of orb web orientation and spider size on prey retention. *Bulletin of the British Arachnological Society* 8:45–48.
- Eberhard, W.G. 1990. Function and phylogeny of spider webs. *Annual Review of Ecology and Systematics* 21:341–372.
- Eberhard, W.G., I. Agnarsson & H.W. Levi. 2008. Web forms and phylogeny of theridiid spiders (Araneae: Theridiidae): chaos from order? *Systematics and Biodiversity* 6:415–475.
- Field, A. 2005. *Discovering Statistics Using SPSS*, 2nd edition. Sage Publications, London, UK.
- Foelix, R.F. 1996. *Biology of Spiders*, 2nd edition. Oxford University Press, Oxford, UK.
- Foelix, R.F. 2011. *Biology of Spiders*, 3rd edition. Oxford University Press, Oxford, UK.
- Gillespie, R.G. & T. Caraco. 1987. Risk-sensitive foraging strategies of two spider populations. *Ecology* 68:887–899.
- Graham, D.L. 1997. Spider webs and windows as potentially important sources of hummingbird mortality. *Journal of Field Ornithology* 68:98–101.
- Grasshoff, M. 1984. Die Radnetzspinnen-Gattung *Caerostris* (Arachnida: Araneae). *Revue Zoologique Africaine* 98:725–765.
- Gregorič, M., R. Kostanjšek & M. Kuntner. 2010. Orb web features as taxonomic characters in *Zygiella* s.l. (Araneae, Araneidae). *Journal of Arachnology* 38:319–327.
- Griswold, C.E., J.A. Coddington, G. Hormiga & N. Scharff. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbicularia: Deinopoidea, Araneioidea). *Zoological Journal of the Linnean Society* 123:1–99.
- Harmer, A.M.T. 2009. Elongated orb-webs of Australian ladder-web spiders (Araneidae: *Telaprocera*) and the significance of orb-web elongation. *Journal of Ethology* 27:453–460.
- Harmer, A.M.T. & V.W. Framenau. 2008. *Telaprocera* (Araneae: Araneidae), a new genus of Australian orb-web spiders with highly elongated webs. *Zootaxa* 1956:59–80.
- Herberstein, M.E. & I.M. Tso. 2000. Evaluation of formulae to estimate the capture area and mesh height of orb webs (Araneioidea, Araneae). *Journal of Arachnology* 28:180–184.
- Herberstein, M.E. & I.M. Tso. 2011. Spider webs: evolution, diversity and plasticity. Pp. 57–98. *In* *Spider Behaviour: Flexibility and Versatility*. (M.E. Herberstein, ed.). Cambridge University Press, Cambridge, UK.
- Jäger, P. 2007. Spiders from Laos with descriptions of new species (Arachnida: Araneae). *Acta Arachnologica* 56:29–58.
- Knoflach, B. & A. Van Harten. 2000. Palpal loss, single palp copulation and obligatory mate consumption in *Tidarren cuneolatum* (Tullgren, 1910) (Araneae, Theridiidae). *Journal of Natural History* 34:1639–1659.
- Kuntner, M. 2005. A revision of *Herennia* (Araneae: Nephilidae: Nephilinae), the Australasian 'coin spiders'. *Invertebrate Systematics* 19:391–436.
- Kuntner, M. 2007. A monograph of *Nephilengys*, the pantropical 'hermit spiders' (Araneae, Nephilidae, Nephilinae). *Systematic Entomology* 32:95–135.
- Kuntner, M. & I. Agnarsson. 2009. Phylogeny accurately predicts behaviour in Indian Ocean *Cliatastra* spiders (Araneae: Nephilidae). *Invertebrate Systematics* 23:193–204.
- Kuntner, M. & I. Agnarsson. 2010. Darwin's bark spider: web gigantism in a new species of bark spider from Madagascar (Araneidae: *Caerostris*). *Journal of Arachnology* 38: 346–356.
- Kuntner, M., J.A. Coddington & G. Hormiga. 2008a. Phylogeny of the extant nephilid orb-weaving spiders (Araneae, Nephilidae) – testing morphological and ethological homologies. *Cladistics* 24:147–217.



- Kuntner, M., C.R. Haddad, G. Aljančić & A. Blejec. 2008b. Ecology and web allometry of *Chitactra ireneae*, an arboricolous African orbweaving spider (Araneae, Araneoidea, Nephilidae). *Journal of Arachnology* 36:583–594.
- Kuntner, M., I. Agnarsson & M. Gregorić. 2009a. Nephilid spider cunuch phenomenon induced by female or rival male aggressiveness. *Journal of Arachnology* 37:266–271.
- Kuntner, M., J.A. Coddington & J.M. Schneider. 2009b. Intersexual arms race? Genital coevolution in nephilid spiders (Araneae, Nephilidae). *Evolution* 63:1451–1463.
- Kuntner, M., S. Krajič-Fišer, J.M. Schneider & D. Li. 2009c. Mate plugging via genital mutilation in nephilid spiders: an evolutionary hypothesis. *Journal of Zoology* 277:257–266.
- Kuntner, M., M. Gregorić & D. Li. 2010a. Mass predicts web asymmetry in *Nephila* spiders. *Naturwissenschaften* 97:1097–1105.
- Kuntner, M., S. Krajič-Fišer & M. Gregorić. 2010b. Ladder webs in orb-weeb spiders: ontogenetic and evolutionary patterns in Nephilidae. *Biological Journal of the Linnean Society* 99:849–866.
- Levi, H.W. 1970. The *navilla* group of the orbweaver genus *Eriophora* in North America (Araneae: Araneidae). *Psyche* 77:280–302.
- Nakata, K. & S. Zschokke. 2010. Upside-down spiders build upside-down orb webs: web asymmetry, spider orientation and running speed in *Cyclosa*. *Proceedings of the Royal Society B* 277:3019–3025.
- Nentwig, W. 1985. Prey analysis of four species of tropical orbweaving spiders (Araneae: Araneidae) and a comparison with araneids of the temperate zone. *Oecologia* 66:580–594.
- Opell, B.D. 1999. Redesigning spider webs: Stickiness, capture area and the evolution of modern orb-webs. *Evolutionary Ecology Research* 1:503–516.
- Peloso, P.L. & V.P. de Sousa. 2007. Predation on *Todirostrum cinereum* (Tyrannidae) by the orb-web spider *Nephilengys cruentata* (Araneae, Nephilidae). *Revista Brasileira de Ornitologia* 15: 461–463.
- Peters, H. 1937. Studien am netz der kreuzspinne (*Aranea diadema*). 1. Die Grundstruktur des Netzes und Beziehungen zum Bauplan des Spinnenkörpers. *Morphologie und Ökologie der Tiere* 33:128–150.
- Platnick, N.I. 2010. The World Spider Catalog, Version 11.0. The American Museum of Natural History, New York. Online at <http://research.amnh.org/entomology/spiders/catalog/>
- Rao, D., K. Cheng & M.E. Herberstein. 2008. Stingless bee response to spider webs is dependent on the context of encounter. *Behavioral Ecology and Sociobiology* 63:209–216.
- Rao, D., M. Webster, A.M. Heiling, M.J. Bruce & M.E. Herberstein. 2009. The aggregating behaviour of *Argiope radon*, with special reference to web decorations. *Journal of Ethology* 27:35–42.
- Risch, P. 1977. Quantitative analysis of orb web patterns in four species of spiders. *Behavior Genetics* 7:199–238.
- Robinson, M.H. & B. Robinson. 1972. The structure, possible function and origin of the remarkable ladder-web built by a New-Guinea orbweb spider (Araneae: Araneidae). *Journal of Natural History* 6:687–694.
- Robinson, M.H. & B. Robinson. 1974. The biology of some *Argiope* species from New Guinea: predatory behavior and stabilimentum construction (Araneae: Araneidae). *Zoological Journal of the Linnean Society* 54:145–159.
- Robinson, M.H. & B. Robinson. 1980. Comparative studies of the courtship and mating behavior of tropical araneid spiders. *Pacific Insects* 36:35–218.
- Rodriguez-Girones, M.A., C. Guadalupe & J. Moya-Larano. 2010. Silk elasticity as a potential constraint on spider body size. *Journal of Theoretical Biology* 266:430–435.
- Sakai, W.H. 2007. Long-billed hermit (*Phaethornis superciliosus*) caught in golden orb-spider (*Nephila clavipes*) web. *Ornitologia Neotropical* 18:117–119.
- Sandoval, C.P. 1994. Plasticity in web design in the spider *Parawixia bistriata*: a response to variable prey type. *Functional Ecology* 8:701–707.
- Sensenig, A., I. Agnarsson & T.A. Blackledge. 2010. Behavioural and biomaterial coevolution in spider orb webs. *Journal of Evolutionary Biology* 23:1839–1856.
- Scharff, N. & J.A. Coddington. 1997. A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). *Zoological Journal of the Linnean Society* 120:355–434.
- Sherman, P.M. 1994. The orb web—an energetic and behavioral estimator of a spider's dynamic foraging and reproductive strategies. *Animal Behaviour* 48:19–34.
- Thomas, A.L.R., K.G. Taylor, R.B. Srygley, R.L. Nudds & R.J. Bomphrey. 2004. Dragonfly flight: free-flight and tethered flow visualizations reveal a diverse array of unsteady lift-generating mechanisms, controlled primarily via angle of attack. *Journal of Experimental Biology* 207:4299–4323.
- Timm, R.M. & M. Losilla. 2007. Orb-weaving spider, *Argiope savignyi* (Araneidae), predation on the proboscis bat *Rhynchonycteris naso* (Emballonuridae). *Caribbean Journal of Science* 43:282–284.
- Uhl, G. & F. Vollrath. 1998. Little evidence for size-selective sexual cannibalism in two species of *Nephila* (Araneae). *Zoology* 101: 101–106.
- Venner, S. & J. Casas. 2005. Spider webs designed for rare but life-saving catches. *Proceedings of the Royal Society B* 272:1587–1592.
- Wiehle, H. 1927. Beiträge zur Kenntnis des Radnetzbaues der Epeiriden, Tetragnathiden und Uloboriden. *Zeitschrift für Morphologie und Ökologie der Tiere* 8:468–537.
- Wiehle, H. 1928. Beiträge zur Biologie der Araneen, insbesondere zur Kenntnis des Radnetzbaues. *Zeitschrift für Morphologie und Ökologie der Tiere* 8:468–537.
- Wiehle, H. 1929. Weitere Beiträge zur Biologie der Araneen, insbesondere zur Kenntnis des Radnetzbaues. *Zeitschrift für Morphologie und Ökologie der Tiere* 15:262–308.
- Wiehle, H. 1931. Neue Beiträge zur Kenntnis des Fanggewebes der Spinnen aus den Familien Argiopidae, Uloboridae und Theridiidae. *Zeitschrift für Morphologie und Ökologie der Tiere* 22:349–400.
- Zschokke, S. 2002. Form and function of the orb-web. Pp. 99–106. *In* European Arachnology 2000. (S. Toft & N. Scharff, eds.). Aarhus University Press, Aarhus, Denmark.

## ELECTRONIC SUPPLEMENTARY MATERIAL

*Caerostris* supplementary video 1 (<http://www.nephilidae.com/videos/videos.htm>): Dragonfly introduced into subadult female *C. darwini* web. Note bite-wrap attack behavior and spider carrying the prey to hub in its chelicerae.

*Caerostris* supplementary video 2 (<http://www.nephilidae.com/videos/videos.htm>): Dragonfly introduced into female *C. darwini* web. Note spider lifting the prey towards hub while the prey is still attached to other web parts.

*Caerostris* supplementary video 3 (<http://www.nephilidae.com/videos/videos.htm>): Kleptoparasitic flies approaching female *C. darwini* and her prey.